

NEOGENE FLORISTIC AND VEGETATIONAL HISTORY OF THE PACIFIC NORTHWEST

JACK A. WOLFE

The Neogene fossil plant assemblages of the Pacific Northwest are more numerous and more completely studied than the Neogene assemblages of any other area of North America (fig. 1). Most of the work has been based on the study of plant megafossils—particularly leaves—which provide a valid basis for the reconstruction of lineages and hence floristic history. The increasing body of palynologic data, on the other hand, provides an insight into vegetational history, which is difficult to reconstruct from megafossils that represent largely the specialized streamside and lakeside vegetation. Both megafossil and microfossil assemblages typically represent ligneous plants, although microfossil assemblages include more representatives of herbaceous plants than do megafossil assemblages. This report will thus primarily concern woody plants.

By piecing together lineages and by analyzing the vegetational types in which the lineages have lived, it is possible to understand the development of vegetation in terms of its floristic elements. Proponents of various “geofloral” concepts have unfortunately confused flora and vegetation, which inherently leads to a confusion of floristic and vegetational history. It is extremely improbable from the genetic and physiological viewpoint that many lineages could have remained in association throughout the Tertiary; that is, that a given vegetational type remained floristically unchanged (Mason, 1947; MacGinitie, 1962; Wolfe, 1964). Recent work has indeed shown that many “Madro-Tertiary” elements in Nevada represent lineages that were present earlier in the mesic Miocene vegetation of the Pacific Northwest (Wolfe, 1964). Work in Alaska has also shown that the concept of an “Arcto-Tertiary Geoflora” is invalid (Wolfe, et al., 1966; Wolfe, 1966; 1969; Wolfe and Leopold, 1967; Wahrhafting, et al., 1969; Hopkins, et al., in press). The discussion of the Neogene of the Pacific Northwest involves an understanding of the history not only of that area but of much of northwestern North America.

I wish to thank H. D. MacGinitie and H. E. Schorn, University of California, Berkeley, and E. B. Leopold, U.S. Geological Survey, for their helpful discussions of the subjects covered in this report and for their critical reading of the manuscript. K. M. Piel, Union Oil Company of California, kindly provided his unpublished pollen count for the late Miocene Quesnel diatomite of British Columbia.

Publication of this paper has been authorized by the Director, U.S. Geological Survey.

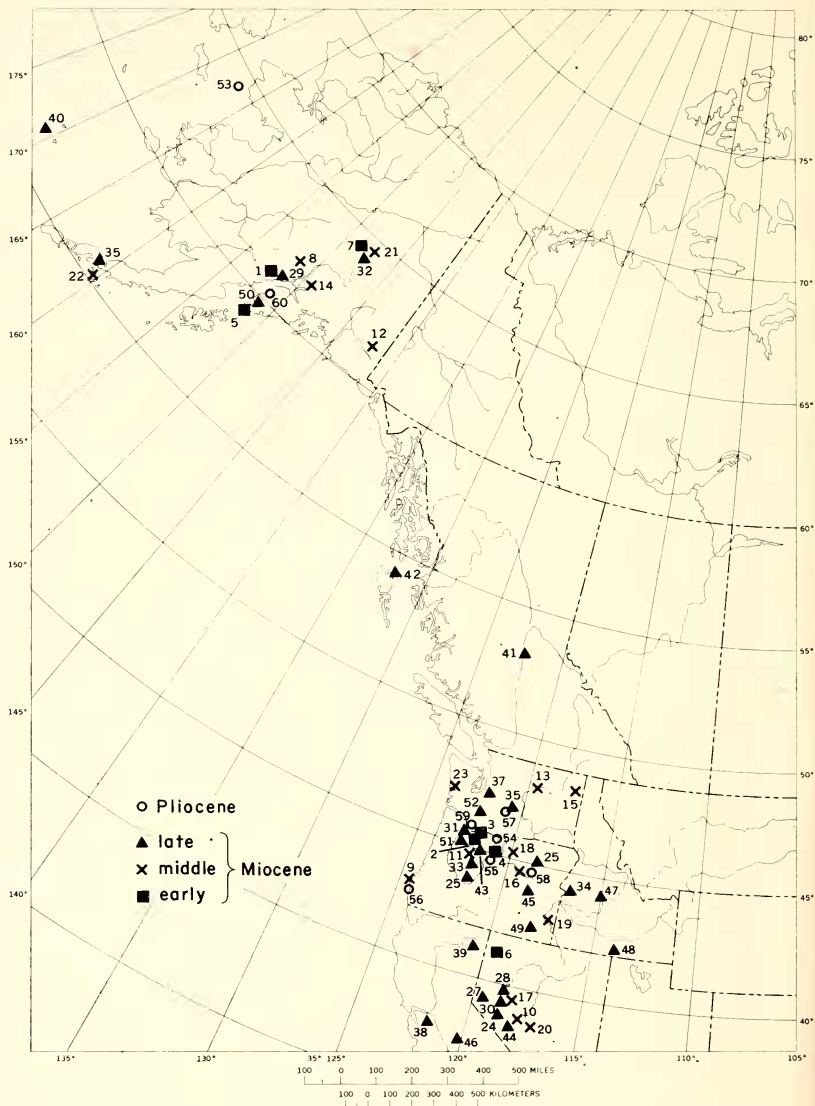


FIG. 1. Location of some Neogene and early Pleistocene assemblages in northwestern North America. Numbers correspond to assemblages as follows:

Early Miocene

- | | | |
|----------------------|-------------------|---------------------|
| 1. Capps Glacier | 2. Collawash | 3. Eagle Creek |
| 4. Maupin | 5. Seldovia Point | 6. Upper Cedarville |
| 7. Upper Healy Creek | | |

METHODS OF DETERMINING VEGETATION

The paleobotanist, after completing identification of the fossils from a given assemblage or series of assemblages, has at least a partial list of the flora. The significance of such a list in terms of vegetation is not agreed on by all paleobotanists. Most paleobotanists working on Tertiary assemblages of western North America have used a two-fold approach to determine vegetation: 1, a strict application of uniformitarianism to the tolerances of a given lineage, genus, or family (i.e., tolerances have not changed through time), and 2, counts of the megafossils.

That lineages have had different tolerances in the past than at present should be obvious from theoretical considerations. Assuming that the dicotyledons, for example, at one time evolved in a limited area that had a limited number of habitats and climates, during the spread outward from such an area the organisms in any lineage would have met new environmental conditions; the same reasoning can be applied to the lineages comprising any genus or subgenus. The fact that the dicotyledons today occupy an extremely wide range of habitats is an indication that lineages are capable of adapting to new environmental conditions. The fossil record in fact supports such a concept of changing tolerances: one lineage of *Pterocarya*, for example, first appears in North America during the Eocene in subtropical and tropical forests (Wolfe, 1968). During the Oligocene, the lineage is represented in tropical forest during the early part of that epoch, but by the late Oligocene it was present in warm temperate vege-

Middle Miocene

- | | | |
|-------------------|----------------|------------------|
| 8. Cache Creek | 9. Cape Blanco | 10. Fingerrock |
| 11. Fish Creek | 12. Frederika | 13. Grand Coulee |
| 14. Houston | 15. Latah | 16. Mascall |
| 17. Middlegate | 18. Monument | 19. Rockville |
| 20. San Antonio | 21. Suntrana | 22. Unga Island |
| 23. Wishkaw River | | |

Late Miocene

- | | | |
|---------------------|---------------------|----------------------|
| 24. Aldrich Station | 25. Blue Mountains | 26. Brock Road |
| 27. Chalk Hills | 28. Chloropagus | 29. Chuitna River |
| 30. Fallon | 31. Faraday | 32. Grubstake |
| 33. Hidden Lake | 34. Hog Creek | 35. Lower Ellensburg |
| 36. Marble Point | 37. Mashel | 38. Neroly |
| 39. Pit River | 40. Pribilof Canyon | 41. Quesnell |
| 42. Skonun | 43. Skunk Creek | 44. Stewart Spring |
| 45. Stinking Water | 46. Table Mountain | 47. Thorn Creek |
| 48. Trapper Creek | 49. Trout Creek | 50. Type Homerian |
| 51. Weyerhauser | 52. Wilkes | |

Pliocene and early Pleistocene

- | | | |
|---------------------|-----------------------|-----------------|
| 53. Bering Platform | 54. Dalles | 55. Deschutes |
| 56. Elk River | 57. Middle Ellensburg | 58. Rattlesnake |
| 59. Troutdale | 60. Type Clamgulchian | |

tation (Wolfe, 1959). During the early and middle Miocene, the lineage participated in the Mixed Mesophytic forest, and during the late Miocene the lineage is represented only in conifer forest. *Pterocarya* is today represented only in broad-leaved deciduous forests. In most instances, of course, tolerances of the Neogene representatives of a given genus or lineage probably more closely approximate the present tolerances of the genus or lineage than do the Paleogene representatives. Note, however, that *Chamaecyparis nootkatensis* participated in vegetation that represents a conifer-live oak association during the late Miocene in southwestern Nevada (Wolfe, 1964); clearly *C. nootkatensis* included during the late Miocene physiological races that are no longer extant. Uniformitarianism should be applied cautiously to vegetational reconstructions.

If, of course, the "associational method" of determining the flora is utilized, such anomalous associations as that of *Chamaecyparis nootkatensis* and *Quercus chrysolepis* will not be known. The "holotype" of the associational method of determination (Cain, 1944, p. 43) is in fact an excellent demonstration of the weakness of the method. Knowlton (1902) originally described *Cinnamomum bendirei* from the Bridge Creek assemblage of Oregon. Chaney (1927), however, interpreted this assemblage as a redwood forest and thus considered *Cinnamomum* an incongruous element. He therefore transferred Knowlton's species to *Philadelphus*, which would be expected in a redwood forest. Brown (1940) pointed out that the leaves morphologically could not be *Philadelphus* but had the diagnostic characters of Lauraceae; he thus transferred the species to *Sassafras*. This transfer was ignored by Chaney (194b, p. 350), who still considered that *Philadelphus* was a better choice for a redwood forest. After the discovery of the living *Metasequoia* and the realization that the Bridge Creek assemblage contained not *Sequoia* but rather *Metasequoia*, Chaney (1952) accepted Brown's transfer of the species to *Sassafras*. The leaves, however, have the small areoles lacking branched, freely ending veinlets and the continuous marginal vein of *Cinnamomum*, *Lindera*, and *Neolitsea*; *Sassafras* has large areoles intruded by branching veinlets and lacks a marginal vein (Wolfe, 1960). Knowlton's determination was more valid than either Chaney's or Brown's.

The second widely used method of reconstructing past vegetation is through the use of leaf counts. The basic assumption of this method is that the representation of leaves in a fossil bed is proportional to the representation of the plants that bore them in the ancient forests. Chaney (1959) has discussed the variables affecting such an assumption, and was forced to the conclusion (p. 46) that the assumption was perhaps valid only for generalities. Without any statistical basis, Chaney (1959, p. 46) stated: "I believe that any species that has provided as much as one-fifteenth [about 7 percent] of the record of foliage and fruit in a fossil flora must have been numerous enough to be considered abundant in the forest . . ." Whether Chaney's belief is valid is, of course, unknown.

It is extremely doubtful that the relative representation of plant mega-

fossils is significant in reconstructing ancient vegetation. Megafossil assemblages contain an overrepresentation of fluvatile and lacustrine species that grew at or near the site of deposition (MacGinitie, 1953, p. 46; Fægri and Iversen, 1964, p. 39). As yet, no one has demonstrated any sizable correlation between the relative representation of organisms and the relative representation of their larger organs either on the forest floor or at the sites of deposition. One attempt to do so is that of Chaney (1924). The correlation coefficients he obtained were indeed sufficiently high to indicate that leaf counts might be valuable in reconstructions of vegetation. The only species for which Chaney gave the raw data is *Alnus rubra* [= *A. oregona*], the coefficient computed was 0.49. Note, however, that negative matches, situations in which neither organisms or remains of this species were found, were included in the computations. Such an inclusion hardly seems justifiable; the coefficient would be even higher if a worker included negative matches from Nevada, where the species does not grow. Recomputation of the correlation coefficient after elimination of all negative matches yields a coefficient of 0.35, i.e., very close to a universe in which no correlation exists. I conclude that although there is a slight correlation, it is insufficient for leaf counts to be considered useful in the reconstruction of vegetation.

Fossil leaves are, however, not entirely useless in determining vegetation. The physiognomic features of foliage are largely independent of taxonomy and appear to be highly sensitive to the environment (Richards, 1952, p. 154). The correlation between vegetational types and the leaf margin—whether entire or nonentire—is striking (Bailey and Sinnott, 1915, 1916). Several paleobotanists have applied this correlation to vegetational interpretations of fossil assemblages. In general, in a mesic climate, the percentages of species that have entire margined leaves can be correlated to vegetational type as follows:

- 76+ Tropical Rain forest
- 57-75 Paratropical Rain forest (extratropical rain forest of Wang, 1961; Subtropical Rain forest of Richards, 1952)
- 40-56 Subtropical forest
- 10-35 Temperate forest

Summer dryness and extreme winter low temperatures increase the percentage for the temperate forest; this increase is probably related to the physiological aridity of both far northern and truly arid climates. In Alaska, for example, the leaf margin percentage is 42, but a large number of the woody dicot species that have entire margins are thick- and small-leaved Ericaceae. The leaves of species of mid latitude, arid environments show similar adaptations. A consideration of leaf size should, therefore, be considered along with the type of leaf margin.

For Neogene assemblages, the microfossil assemblages are probably an excellent source of data for reconstructions of vegetation. Microfossil as-

semblages do not, insofar as the pollen of woody plants is concerned, represent local vegetation only; the pollen rain of a given region appears to be rather uniform and reflects the predominant vegetation type in the region (Davis and Goodlett, 1960). The variables affecting the interpretation of a pollen diagram have been and are being investigated; corrective factors that take into account many of the variables have been proposed (see for example, Fægri and Iversen, 1964, p. 99-123). Although some of the variables, for example, amount of pollen production, may have changed for various genera, the comparison of two approximately isochronous spectra or diagrams should yield a reasonable idea of the distribution of vegetational types during that interval of time. It should be emphasized, however, that interpretation of a single spectrum can be highly misleading; in a region of active volcanism, for example, one major eruption could drastically change the regional vegetation and hence pollen rain. Reconstruction of even a short diagram through several feet of section should help eliminate the effect of such short term changes in vegetation.

EFFECT OF ALTITUDE

Some workers have argued that previous interpretations of vegetational and floristic history in the Pacific Northwest have failed to take into account the varying altitudes at which the fossil assemblages lived. Thus Axelrod (1964) considered that a particular group of assemblages from the Pacific Northwest is isochronous and of middle Miocene age; these assemblages purportedly show a strong floristic and vegetational zonation according to altitude. The only method of testing the validity of Axelrod's conclusion is to demonstrate the contemporaneity of the assemblages. Various data—mammalian, radiometric, diatom, freshwater molluscan, and stratigraphic—all of which are high reliable for determining relative ages in the Neogene rocks of the Pacific Northwest, are available for several of these assemblages:

Assemblage	Basis for age assignment	Altitude ⁵	Probable "absolute" age
Trapper Creek	diatoms, mollusks, stratigraphy ¹	3,000 ft.	11-12 m.y.
Trout Creek	radiometric ²	2,300	13.1 m.y.
Mascall	radiometric ²	1,500	15.4 m.y.
Upper Cedarville	radiometric ²	1,100	19.8 m.y.
Rockville ("Succor Creek," in part)	radiometric ²	600	16.7 m.y.
Grand Coulee	radiometric ⁴	250	15.7-16.8 m.y.
Latah	radiometric ^{3,4}	250	15.5-20.6 m.y.

¹ Mapel and Hail, 1959.

² Evernden and James, 1964.

³ Obradovich, unpub. data.

⁴ Gray and Kittleman, 1967.

⁵ Axelrod, 1964.

These data illustrate that age, not altitude, is the important factor. The early Miocene Upper Cedarville flora represents a cool time interval as compared with the warmer ("lower altitude") middle Miocene assemblages such as the Grand Coulee, Latah, Mascall, and Rockville (Wolfe and Hopkins, 1967). The age of the Upper Cedarville has been a matter of considerable discussion. I (1964), for example, have considered this assemblage to be of late Miocene age. The problem arises from the fact that LaMotte (1936) included in this flora material from '49 Camp, where the early Miocene radiometric age was obtained, and from the Pit River area many miles to the east. The Pit River assemblage contains *Platanus dissecta* Lesq., which is a typically late Miocene species. The Upper Cedarville ('49 Camp) and Pit River are here considered as distinct floras. The Rockville-Succor Creek problem is analogous to that of the Upper Cedarville-Pit River. The Succor Creek (late Miocene) and Rockville (middle Miocene) assemblages are here considered as distinct.

The late Miocene assemblages likewise represent a cooler time interval than do the middle Miocene assemblages. These middle and late Miocene assemblages do show a gradation from lower to higher, but this gradation is stratigraphic and not altitudinal.

EARLY MIOCENE

The concept of early Miocene varies from one paleontological discipline to another. The mammalian workers use the term Arikareean for this interval; radiometric dates indicate a duration for the Arikareean from about 21 to 25 or 26 million years ago (Evernden, et al., 1964). The foraminiferal workers, on the other hand, consider their Saucian Stage to be basal early Miocene, and the base of this stage has a radiometric age of 22.5 million years (Turner, 1968). The moluscan paleontologists consider their Vaqueros "stage" to be of earliest middle Miocene age and this is thought to be equivalent in the foraminiferal sequence to the Saucian stage. The base of the Miocene in western North America thus can be placed from about 23 to 28 million years, depending on which biostratigraphic framework is accepted. The only plant assemblages in this time interval (early Miocene) that have radiometric dates are the small Maupin assemblage, the upper member of the John Day Formation, which is younger than 23 million years (Evernden, et al., 1964) and the Upper Cedarville with an age of 19.8 million years (Evernden and James, 1964). These assemblages are, on paleobotanical grounds, correlative to the Miocene zone 2 of Wolfe (1962) and to the lower part of the Seldovian Stage of the paleobotanical geochronology. The lower Seldovian assemblages which are the oldest under consideration here may thus not be basal Miocene and may represent only the later part, 19 to 23 or 24 million years, of the early Miocene.

The known lower Seldovian assemblages are well represented in Alaska and in conterminous United States. In Alaska, they include the Seldovia Point, Capps Glacier, and Upper Healy Creek assemblages (Wolfe, et al.,

1966; Wolfe, 1966; Wahrhaftig, et al., 1969). A total of about 70 megafossil entities is known, and the pollen floras have also been extensively studied. In conterminous United States, aside from the Maupin (Wolfe, unpublished data) and Upper Cedarville (LaMotte, 1936), lower Seldovian assemblages include the Collawash (Wolfe, unpublished data) and Eagle Creek (Chaney, 1920). Approximately 160 megafossil entities are known, but, except for the Collawash, the microfossil assemblages apparently have not been studied.

The Alaskan assemblages are preserved in rocks that, for the most part, were deposited in large coal basins at low altitudes. The Upper Healy Creek beds were deposited at least 300 miles from the coast, and the Capps Glacier assemblage may have been only about 100 to 150 miles from the coast. The Seldovia Point assemblage was nearer to the coast than the other two assemblages but the beds containing their assemblage were deposited in a valley in an area of moderate relief (Wolfe, et al., 1966).

The topographic setting of the assemblages in Oregon is known with reasonable certainty. The basalts of the Columbia River Group buried and thus preserved some of the early Miocene topography in northwestern Oregon. At the time, the Cascades were probably more than 1,500 feet in height (Peck, et al., 1964, p. 28); the Collawash beds are at about the altitude at which the basalts thinned out against the range. To the north, in the area of Eagle Creek deposition, the basalts attain a thickness of about 2,500 feet. The distribution and thickness of the basalts thus indicates that the Eagle Creek assemblage probably was in a broad valley not far above sea level, whereas the Collawash assemblage was at about 2,500 feet elevation on the northern margin of the Cascade Range in Oregon. The original elevation of the Maupin assemblage is somewhat uncertain, but the small size of the assemblage makes its vegetational and floristic significance impossible to evaluate at this time.

The original elevation of the Upper Cedarville beds is extremely uncertain; certainly northwestern Nevada had a considerable elevation even in the early Miocene, but an altitudinal interpretation based on geologic data would be highly conjectural.

FLORA. The lower Seldovian flora is known to contain at least 180 megafossil species, and, combined with the microfossil floras, over 200 species are represented. The flora is particularly rich in species of Taxodiaceae, Salicaceae, Juglandaceae, Betulaceae, Fagaceae, Rosaceae, and Aceraceae; also typically present are *Ulmas*, *Zelkova*, *Cocculus*, *Liquidambar*, and *Platanus*.

The sources of many lineages in the lower Seldovian floras are known with reasonable certainty. One source is earlier vegetation of the Pacific Northwest; the lineages occurred in vegetation that represented Paratropical Rain forests, i.e., similar to the vegetation of lowland Taiwan and Hong Kong, or Subtropical forests. These lineages have displayed a

considerable adaptability to changes in climate. Another source is the Paleogene temperate to marginally subtropical upland assemblages along the Rocky Mountains (Wolfe, 1960); some of these lineages had already appeared in the Pacific Northwest by the time that temperate vegetation occupied this area in the later Oligocene. A third, although minor, source is represented by lineages that first appear in the later Oligocene temperate vegetation of Alaska.

The lineages of Fagaceae for the most part are of unknown descent. One of the particularly striking features of Miocene as compared with older floras is the presence of "lobed" oaks, particularly the black oaks. The black "lobed" oaks are apparently restricted to North America, although Chelebaeva (1968) has referred a fragmentary specimen from the middle Miocene of Kamchatka to this group. The predecessors of the "lobed" black oaks must almost certainly be within the other members of the subgenus *Erythrobalanus*, and possibly forms such as *Quercus peritula* Cocker. from the marginally subtropical Florissant assemblage of the early Oligocene of the Rocky Mountains or *Q. pregrahamii* MacG. from the subtropical Weaverville assemblage of the late Oligocene of California may be ancestral. The origin of the "lobed" white oaks is even more problematic. MacGinitie (1953) considers the subgeneric assignment of the Florissant *Q. lyratiformis* Cocker. to be dubious, and this is the only pre-Miocene material from North America known to me that has been referred to *Leucobalanus*. The close relationship between the extant east American and the Miocene west American members of *Leucobalanus* indicates the probability that there was a common source in the Oligocene of the Rocky Mountains.

Some regional floristic differentiation is apparent in the early Miocene of northwestern North America. Most species of Salicaceae, for example, are distinct between Alaska and the Pacific Northwest. Rosaceae are more diverse in the Pacific Northwest and Lauraceae are unknown in Alaska. The Alaskan flora has a definite Asian element that did not reach the Pacific Northwest: *Acer fatisiifolia*, *A. ezoanum*, *Kalopanax*, *Ulmus longifolia*, *Populus reniformis*. More than half the known Alaskan lower Seldovian species are, however, also known in the Pacific Northwest, thus indicating that the two areas should be considered as parts of the same floristic province during the early Miocene.

Altitudinal zonation of the flora in the Pacific Northwest does not appear to have been pronounced during the early Miocene. Most species known from the low altitude Eagle Creek flora are also known in the upland Collawash flora. Considering the little latitudinal floristic zonation during the early Miocene, it should be expected that altitudinal floristic zonation would also be slight.

VEGETATION. The vegetation of the early Seldovian of northwestern North America was broad-leaved deciduous. An apparently continuous deciduous forest extended from Japan and northern China north into

Alaska and south into the Pacific Northwest. Evergreens were an important part of this forest; coniferous evergreens became increasingly important in the north and broad-leaved evergreens in the south.

The Alaskan pollen assemblages from the Cook Inlet region indicate that locally the conifers such as *Picea* were present in the lowland forest—presumably because of the cool summers (Wolfe and Leopold, 1967). In the interior of Alaska, however, only deciduous conifers of Taxodiaceae appeared in significant numbers with the broad-leaved deciduous plants. Broad-leaved evergreens were apparently rare in Alaska. The leaf margin percentage for the Alaskan lower Seldovian flora is 15, i.e., similar to that for the temperate forest of the Mid-Atlantic Staes and the northern border of the Mixed Mesophytic forest in China today.

In the Pacific Northwest, broad-leaved evergreens were more diverse and include: *Quercus*, *Magnolia*, *Cinnamomum*, *Litsea*, *Persea*, *Umbrellularia*, *Exbucklandia*, *Cercocarpus*, *Lyonothamnus*, *Garrya*, and *Arbutus*. The leaf margin percentage for a large assemblage such as the Collawash is 25, i.e., similar to that for the region occupied by the Mixed Mesophytic forest in central China. The pollen assemblages from the Collawash beds contain only minor amounts of *Picea*, indicating that coniferous forest was not present even at 2,500 feet altitude. In eastern Asia today the Mixed Mesophytic forests has a latitudinal range of about 14°, but in western North America this vegetational type spanned at least 25° of latitude; even in the early Miocene latitudinal zonation of vegetation was much less pronounced than today.

MIDDLE MIOCENE

In this report, the term middle Miocene denotes an interval from about 14 or 15 to about 19 million years age. This interval is equivalent to the Hemingfordian and early Barstovian ages of the mammalian paleontologists. Assemblages of this age in Alaska include the Unga Island (locs. P9978, P9993 of Burk, 1965), Suntrana (Wahrhaftig, et al., 1969), two assemblages in the Kenai formation, the Houston and Cache Creek (Wolfe, et al., 1966) and the Frederika (Wolfe, unpublished data). In the Pacific Northwest, assemblages of this age include the Fish Creek, Cape Blanco, Wishkaw River, and Monument (Wolfe, unpublished data), as well as published assemblages such as the Latah (see Chaney and Axelrod, 1959, for list of references), Grand Coulee (Berry, 1931), Mascall (Chaney and Axelrod, 1959), and Rockville (Graham, 1965), which is, in part, the Succor Creek flora of some authors. In Nevada, only two middle Miocene assemblages have been described, the Middlegate (Axelrod, 1956) and the Fingerrock (Wolfe, 1964); an additional assemblage is known from the San Antonio Range (Wolfe, unpublished data) and three other assemblages are currently under study by Axelrod. In central California, no assemblages of middle Miocene age have been thoroughly studied.

The depositional setting of the assemblages from Alaska is, with one

exception, lowland. The exception is the Frederika, which is preserved in beds that were deposited in an area of considerable relief. These beds were formed in part because of the damming of the drainage by the first extrusion of the Wrangell lavas (E. M. MacKevett, pers. comm., March 1969).

In the Pacific Northwest, both the Wishkaw River and Cape Blanco assemblages occur in intertonguing marine-nonmarine rocks, and hence represent coastal lowland vegetation. The Fish Creek assemblage occurs in beds that overlie the basalts of the Columbia River Group; presumably the Fish Creek assemblage lived at about the same elevation as the early Miocene Collawash assemblage, i.e., about 2,500 feet. In eastern Oregon, the Monument assemblage, which occurs in beds that are pre-Columbia River Group but post-John Day Formation, probably grew in a region of little relief. The Mascall assemblage probably grew in an upland basin surrounded by considerable relief, to judge from the thick volcanic sequence that grades laterally into the Mascall Formation (Thayer and Brown, 1966). The Latah assemblage occurs in lake beds that were formed by the damming of the drainage by the lavas of the Columbia River Group (Pardee and Bryan, 1926). Pardee and Bryan suggest that the lavas, which are much thicker to the east and south than it is now, i.e., higher than 1,500 to 2,000 feet (A. B. Griggs, pers. comm., March 1969). Geologic data bearing on the original altitude of the Rockville and the Middle Miocene assemblages from Nevada is lacking, although it is presumed that these regions were uplands of at least moderate elevation.

FLORA. The flora of the middle Miocene (upper Seldovian) in Alaska and the Pacific Northwest differs little from that of the early Miocene. An almost complete generic list for the early and middle Miocene is given in Table 1. Almost all lineages in the late Seldovian were also represented in the early Seldovian. Some groups, e.g., Salicaceae, were more diverse in Alaska during the late Seldovian than during the early Seldovian, and possibly this represents diversification of the family. Pinaceae are better represented in the megafossil floras than previously, particularly late in the middle Miocene. A fir related to the extant *Abies bracteata* has an earlier record in the upland conifer forests of the Oligo-Miocene of the Rocky Mountains and makes its first appearance in the Pacific Northwest during the middle Miocene.

In Alaska one of the few upland assemblages of Miocene age, the assemblages from the middle Miocene Frederika Formation, contains a

diversity of Pinaceae in contrast to the lowland Alaskan assemblages. Included in the Frederika assemblage are *Abies*, *Picea*, *Pinus*, and *Tsuga*, which are accompanied by *Pterocarya*, *Fagus*, *Ulmus*, and *Acer*.

Over 230 species and 110 genera of presumed ligneous plants are now known in the early and middle Miocene of northwestern North America. Considering the incompleteness of the fossil record, the richness is impressive. Despite extensive search, about 20 species with highly distinctive leaves from the Collawash assemblage have yet to be identified; it is conceivable that some of the leaves belong to extinct genera analogous to the epibiotic and/or monotypic genera of the extant Mixed Mesophytic forest of eastern Asia.

TABLE 1. COMPOSITION OF THE EARLY AND MIDDLE MIOCENE FLORA OF NORTHWESTERN NORTH AMERICA.

"p" denotes a record based largely or entirely on pollen. PNW = Pacific Northwest.

	No. species				No. species		
	Alaska	PNW	Alaska		PNW		
<i>Ginkgo</i>	1	1	1	<i>Celtis</i>	1	0	1
<i>Cephalotaxus</i>	1	0	1	<i>Ulmus</i>	4	2	3
<i>Abies</i>	4	2p	3	<i>Zelkova</i>	1	1	1
aff. <i>Cedrus</i>	1	p	1	<i>Schoepfia/Anacolosa</i>	1p	0	1p
<i>Keteleeria</i>	1	0	1	<i>Aristolochia</i>	1	0	1
<i>Picea</i>	2	1	2	<i>Cercidiphyllum</i>	1	1	1
<i>Pinus</i>	3	2	3	<i>Clematis</i>	2	0	2
<i>Pseudotsuga</i>	1	p	1	<i>Mahonia</i>	3	0	3
<i>Tsuga</i>	1	3p	0	<i>Cocculus</i>	1	1	1
<i>Chamaecyparis</i>	1	1	0	<i>Liriodendron</i>	1	0	1
<i>Fokienia</i>	1	p	1	<i>Magnolia</i>	1	0	1
<i>Calocedrus</i>	1	0	1	" <i>Laurophyllum</i> "	6	0	6
<i>Thuja</i>	1	1	1	<i>Cinnamomophyllum</i>	1	0	1
<i>Cunninghamia</i>	1	0	1	<i>Sassafras</i>	1	0	1
<i>Glyptostrobus</i>	2	1	1	<i>Hydrangea</i>	1	1	1
<i>Metasequoia</i>	1	1	1	<i>Itea</i>	1?	p	p
<i>Sequoia</i>	1	1	1	<i>Exbucklandia</i>	1	0	1
<i>Taxodium</i>	1	1	1	<i>Fothergilla</i>	1	1	1
<i>Populus</i>	12	7	6	<i>Liquidambar</i>	1	1	1
<i>Salix</i>	13	8	6	<i>Platanus</i>	1	1	1
<i>Comptonia</i>	1	1	0	<i>Amelanchier</i>	2	0	2
<i>Carya</i>	4	3	4	<i>Cercocarpus</i>	1	0	1
<i>Juglans</i>	2	1	1	<i>Crataegus</i>	3	1	3
<i>Pterocarya</i>	4	3	4	<i>Holodiscus</i>	1	0	1
<i>Alnut</i>	7	5	7	<i>Lyonothamnus</i>	1	0	1
<i>Betula</i>	3	2	2	<i>Prunus</i>	3	1	3
<i>Ostrya</i>	3	2	1	aff. <i>Peraphyllum</i>	1	0	1
<i>Ostryopsis</i>	1	1	0	<i>Pyrus</i>	1	0	1
<i>Castanea</i>	1	0	1	<i>Rosa</i>	1	0	1
<i>Castanopsis</i>	1	0	1	<i>Rubus</i>	1	0	1
<i>Fagus</i>	7	2	5	<i>Sorbus</i>	2	1	1
<i>Quercus</i>	11	3	10	<i>Spiraea</i>	1	1	0

	No. species				No. species		
	Alaska	PNW			Alaska	PNW	
<i>Albizzia</i>	1	0	1	<i>Xylonagra</i>	1	0	1p
<i>Cercis</i>	1	0	1	<i>Gordonia</i>	1	0	1
<i>Cladrastis</i>	1	1	1	<i>Idesia</i>	1	0	1
<i>Gymnocladus</i>	1	0	1	<i>Shepherdia</i>	1	1	0
<i>Sophora</i>	1	0	1	<i>Cornus</i>	2	0	2
<i>Ptelea</i>	1	0	1	<i>Nyssa</i>	1	1	1
<i>Ailanthus</i>	1	0	1	<i>Oreopanax</i>	1	0	1
<i>Cedrela</i>	1	0	1	<i>Alangium</i>	1	1	0
<i>Rhus</i>	1	0	1	<i>Clethra</i>	1	0	1
<i>Toxicodendron</i>	1	0	1	<i>Arbutus</i>	2	0	2
<i>Pistacia</i>	1	0	1	<i>Leucothoe</i>	1	0	1
<i>Ilex</i>	4	p	4	<i>Rhododendron</i>	2	1	1
<i>Acer</i>	12	7	8	<i>Diospyros</i>	1	0	1
<i>Aesculus</i>	2?	1	1	<i>Kalopanax</i>	1	1	0
<i>Allophylus</i>	1	0	1	<i>Halesia</i>	1	0	1
<i>Ceanothus</i>	1	0	1	<i>Fraxinus</i>	3	1	3
<i>Colubrina</i>	1	0	1	<i>Catalpa</i>	1	0	1
<i>Karwinskia</i>	1	0	1	<i>Diervilla</i>	1p	1p	0
<i>Sageretia</i>	1	0	1	<i>Symphoricarpos</i>	1	1	0
<i>Zizyphus</i>	1	0	1	<i>Sambucus</i>	1	0	1
<i>Vitis</i>	4	1	3	<i>Viburnum</i>	1?	p	1
<i>Tilia</i>	3	1	2	<i>Clerodendrum</i>	1	0	1

Noteworthy in this flora is a so-called Madro-Tertiary element. Included in this category are:

Quercus (part), *Juglans* (*Rhysocaryon*), *Mahonia*, *Cercocarpus*, *Lyonothamnus*, aff. *Peraphyllum*, *Ceanothus*, *Colubrina*, *Karwinskia*, *Garrya*, *Xylonagra*, and *Arbutus*.

Note that most of these genera formed an important part in the upland forest of the late Miocene of Nevada; although they have been termed "Madro-Tertiary" by some workers, i.e., the lineages supposedly migrated northward into Nevada during the Neogene, the history of the lineages indicate that they were derived from a mesic forest of the Pacific Northwest during the middle to late Miocene interval.

The sources of the Mixed Mesophytic forest of the Miocene of western North America have been briefly touched on in this report (see also discussion by Wolfe, 1969). One significant element that contains both evergreen and deciduous broad-leaved plants was derived at various times during the later Paleogene from the evergreen broad-leaved forests. Several lineages representing genera such as *Quercus* (species that have "unlobed" leaves), *Alnus*, *Carya*, *Pterocarya*, *Magnolia*, *Cocculus*, *Cinnamomophyllum*, *Persea*, and other genera of the "Laurophyllum" type; *Liquidambar*; and *Platanus*, can be traced from the Paratropical Rain or Subtropical forests of the Eocene and earlier Oligocene into the temperate vegetation of the Miocene. A second and major element

that primarily contains deciduous broad-leaved plants was derived during the Eocene and earlier Oligocene from the temperate to marginally subtropical vegetation that lived in the uplands, especially the Rocky Mountains. Lineages that display such a distribution represent, for example, *Populus*, *Salix*, *Sassafras*, *Amelanchier*, *Cercocarpus*, *Crataegus*, *Sorbus*, and *Acer*. A third but minor element was derived from the temperate vegetation of the later Oligocene of Alaska; most of these lineages represent Salicaceae or Betulaceae. Many of the lineages from these various sources diversified after entering the Mixed Mesophytic forest; members of Salicaceae, Judlandaceae, and Rosaceae, exemplify such a pattern.

VEGETATION. As in the early Miocene, the vegetation of northwestern North America was largely broad-leaved deciduous forest. Some zonation of vegetation is evident because broad-leaved evergreens, except for Ericaceae, were absent from Alaska but formed a significant element in the Pacific Northwest. Upland vegetation in the Northwest had only a minor element in Pinaceae, but in Alaska conifers of this family were dominant in the uplands.

The middle Miocene was warmer than the early Miocene. This is indicated by comparing the leaf margin percentages of the upland Collawash assemblage, 25, with those of the upland Fish Creek, 31, and Latah, 32, assemblages. Although the percentages for the Collawash and Latah are not strikingly different, the large size of both assemblages indicates that statistically the percentages are highly reliable. The warming could have brought subtropical vegetation farther north along the coast, and indeed the Cape Blanco assemblage has a leaf margin percentage of 35, which is closely approaching subtropical.

In reference to probable altitudes of the assemblages from central and southwestern Nevada, note that the leaf margin percentage for the San Antonio, Middlegate, and Fingerrock assemblages combined is 19. This is considerably less than the percentages for upland Oregon assemblages such as the Mascall or Fish Creek. Broad-leaved evergreens such as *Exbucklandia*, *Magnolia*, and Lauraceae are lacking in Nevada. I think it highly probable that the Nevada assemblages must have been significantly higher than the known middle Miocene assemblages from the Pacific Northwest, some of which grew at altitudes of at least 2,500 feet, i.e., the Nevada assemblages probably lived at altitudes of 4,000 to 5,000 feet or more. This suggestion takes into account the fact that not only do the Nevada assemblages appear to represent a cooler vegetation than that of the Pacific Northwest, but also that the Nevada assemblages are farther south than those in the Northwest.

LATE MIOCENE

The term late Miocene as used in this report represents the later part of the Barstovian and all the early Clarendonian mammalian ages. In

terms of available radiometric ages, this interval lasted from about 14 to about 10 million years ago. Assemblages for which independent ages are available are, in Alaska, the Grubstake (Wahrhaftig and others, 1969), Pribilof Canyon (Hopkins, et al., in press), and Marble Point (locs. P5182, P9990 of Burk, 1965). The largest assemblages, however, are those from the Kenai Formation—the Chuitna River and those from the type section of the Homerian Stage (Wolfe, 1966). In British Columbia, late Miocene assemblages includes the Skonun (Martin and Rouse, 1966) and the Quesnel (Peil, unpublished data). In the Pacific Northwest this interval is represented by the Mashel, Wilkes, Faraday, Weyerhauser, Skunk Creek, Hidden Lake, and Brock Road assemblages (Wolfe, unpublished data), and by many previously published assemblages: Lower Ellensburg (Smiley, 1963), Stinking Water (Chaney and Axelrod, 1959), Blue Mountains (Chaney and Axelrod, 1959), Trout Creek (Graham, 1965), Thorn Creek (Smith, 1941), Trapper Creek (Axelrod, 1964), Hog Creek (Dorf, 1936), and Pit River (La-Motte, 1936). Not included in this discussion is the small assemblage from the Payette Formation. In Nevada, late Miocene assemblages include the Cloropagus, Fallon, and Aldrich Station (Axelrod, 1956), Chalk Hills (Axelrod, 1962), and Stewart Spring (Wolfe, 1964). In central California, only two late Miocene assemblages have been studied: the Table Mountain (Condit, 1944) and the Neroly (Condit, 1938).

In all instances, the Alaskan late Miocene assemblages represent lowland vegetation, as interpreted from the geologic data. Some were coastal (Pribilof Canyon, Marble Point), some were slightly interior (Chuitna River and type Homerian), and one was several hundred miles in the interior (Grubstake). The Skonun assemblage from the Queen Charlotte Islands was obtained from predominantly marine beds, and thus can be considered coastal lowland. The original altitude of the Quesnel assemblage is unknown, except that this area of British Columbia probably had at least moderate elevation during the late Miocene.

The Pacific Northwest assemblages represent both lowland and upland. The Mashel, Wilkes, Faraday, and Weyerhauser assemblages come from the Puget-Willamette lowland, and geologic evidence does not indicate that during the late Miocene this area was at a different altitude than today. During the late Miocene, the High Cascade Range had not yet developed, the Western Cascades being the only significant upland between the eastern and western Pacific Northwest. The fact that a few thousand feet of middle to late Miocene basalt did not override the Cascade Range in southern Washington is an indication that the Western Cascade Range there had at least moderate elevation, 3,000 feet, at the time of extrusion of the basalts. A chain of volcanoes formed the crest of this range in the central and northern parts of the Cascades in Oregon (Peck, et al., 1964, p. 31). Note that the Brock Road assemblage was situated near the crest of the range, whereas the Skunk Creek and Hid-

den Lake assemblages were east of the crest. All are now west of the crest of the present Cascades.

The topographic setting of the assemblages from eastern Oregon and Idaho cannot be precisely determined. The Hog Creek assemblage was probably in a broad valley of the ancestral Snake River. All the other assemblages, however, were in a broad sense upland. Geologic data are likewise imprecise in interpreting the original altitude of the Nevada assemblages, although they too were upland.

In California, the Table Mountain assemblage, which is now in the foothills of the Sierra Nevada, probably was lower than the present altitude, ca. 2,000 feet. The Neroly assemblage occurs in an intertonguing maine-nonmarine section, and was thus coastal.

FLORA. After the middle Miocene, many genera and species of the Mixed Mesophytic forest became extinct in northwestern North America, and are not found even in the lowland regions west of the Cascade Range; the Faraday, Weyerhauser, Wilkes, and Mashel assemblages represent the flora of the Puget-Willamette lowland. Notably lacking in these assemblages are genera such as *Castanea*, *Schoepfia/Anacolosa*, *Cercidiphyllum*, *Cocculus*, *Magnolia*, *Cinnamomophyllum*, *Laurophyllum*, *Exbucklandia*, and many others that were present even in the upland early and middle Miocene. Specific diversity within genera such as *Carya*, *Fagus*, and *Quercus* was also less in the late than in the early to middle Miocene.

Floristic provincialism was more pronounced during the late Miocene than earlier in the Neogene. A similarity matrix was constructed (table 2) based on comparison of the specific composition of the megafossil assemblages. Five groupings are apparent: Alaska, Columbia Plateau-Cascade Range, Nevada, Puget-Willamette, and California. The first three floristically intergrade. Alaska and Nevada had floras that were more closely related than were the floras of Nevada and California or Nevada and the Puget-Willamette area.

Late Miocene assemblages, particularly those in Alaska, display a greater diversity of *Salix* and Ericaceae than earlier assemblages. From Alaska south to the Columbia Plateau and Nevada conifers were better represented than before. The "Madro-Tertiary" elements were largely restricted to Nevada.

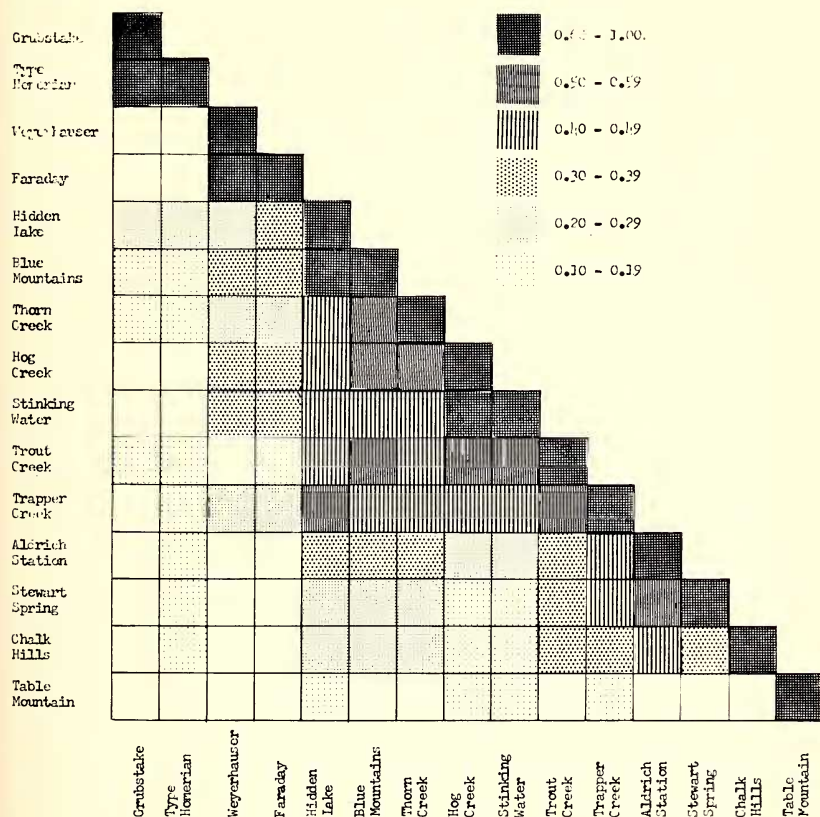
The group that suffered most extinction is composed of lineages that were derived from the paratropical and subtropical vegetation during the later Neogene. The Mixed Mesophytic elements that were derived from the upland assemblages of the Paleogene Rocky Mountains were proportionately better represented in the late than in the early or middle Miocene. Notable exceptions, however, are some lineages of Juglandaceae, Betulaceae, *Liquidambar*, and *Platanus*, all of which were of paratropical or subtropical extraction. These long-ranging lineages were also widely distributed in the Mixed Mesophytic forest and thus probably had broader tolerances than many of their associates.

TABLE 2. SIMILARITY MATRIX OF SOME LATE MIOCENE MEGAFOSSIL ASSEMBLAGES IN NORTHWESTERN NORTH AMERICA.

Coefficient of similarity (or association) is that of Dice and Sørensen as given in Sokal and Sneath (1963, p. 129):

$$S_D = 2n_{JK} / (2n_{JK} + u)$$

where S_D = coefficient of similarity, n_{JK} = number of positive matches, and u = number of negative matches.



The modern aspect of the late Miocene flora is clear. Not only were many extant lineages represented, but in some instances the extant species was represented. Note, however, that many late Miocene lineages have not survived to the present day. One particularly significant example is the lineage represented by aff. *Cedus*; this lineage is represented by cone scales in which the seeds were born entirely on the cone scale as in *Cedrus* but that had a long subtending bract as in *Abies*. At the four localities at which these cone scales have been found, pollen samples typically display an abundance of *Cedrus*-like pollen and presumably the two organs represent the same genus.

It is noteworthy that in the late Miocene some related lineages had attained certain distribution patterns which have been largely maintained to this day, and some lineages had attained a restricted distribution either west or east of the Cascade Range. Thus the lineages of *Alnus incana*, *Betula papyrifera*, and *B. occidentalis* are known only from assemblages that lived to the east of the late Miocene crest of the Cascade Range; the lineages to which *A. oregona* and *A. rhombifolia* belong were, on the other hand, represented only west of the Cascades. In reference to north-south distribution, the probable ancestor of *Holodiscus dumosus* occurs in assemblages that were east and south of the assemblages in which the probable ancestor of *H. discolor* is represented. The lineage of *Betula papyrifera* was largely northern and the lineage of *B. occidentalis* was largely southern. However, some lineages, e.g., that to which *Quercus kelloggi* belongs, were represented both east and west of the Cascades, whereas these lineages are today entirely western.

VEGETATION. The leaf margin percentages for both the Alaska and Nevada assemblages are approximately 30, whereas those for the Puget-Willamette and Columbia Plateau assemblages range from 14 to 24, typically about 17 to 21. The high percentage for Alaska, combined with the small size of the leaves, is interpreted as representing an approach to cold, and hence physiologically arid, conditions; the present percentage for Alaska is 42. In Nevada, however, a summer dry climate had probably set in, which is of course physiologically arid (Wolfe and Hopkins, 1967). Percentages similar to those for Alaska have been obtained for the modern vegetation of the Pacific Northwest. The Puget-Willamette assemblages were probably analogous to the vegetation of the Middle Atlantic states, i.e., temperate broad-leaved deciduous forest.

The extensive amount of pollen data allows an excellent understanding of vegetational regions during the late Miocene (fig. 2). The Alaskan assemblages represent a cool conifer forest, which was floristically more diverse than the present boreal forest. Broad-leaved deciduous plants, other than Betulaceae and Salicaceae, were represented, although sparsely. The Skonun assemblage shows some similarity to the Alaskan assemblages in the high representation of Betulaceae, but the moderate representation of Juglandaceae and Fagaceae indicate a mixed conifer broad-leaved deciduous forest. The Skonun-Mashel-Weyerhauser-Faraday spectra intergrade from the mixed forest in the northern lowlands to a broad-leaved deciduous forest in the southern lowlands. Juglandaceae, Fagaceae, and *Liquidambar* appear to have been the major constituents of the more southern forest. This could be designated a hickory-oak-beech assemblage.

The vegetational differences between the Willamette lowland and the higher elevations in the Cascade Range can be readily determined from the pollen spectra (fig. 3). All upland spectra have large amounts of Pinaceae, particularly aff. *Cedrus* and *Picea*, whereas, except for

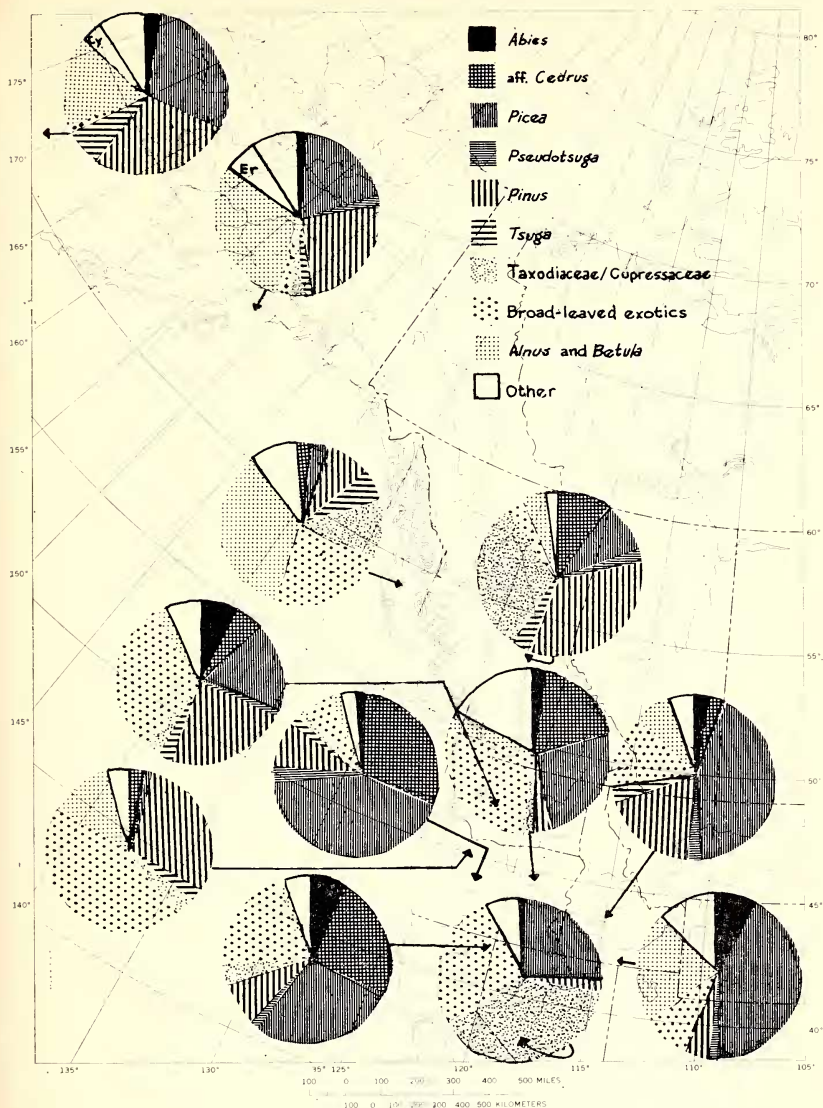
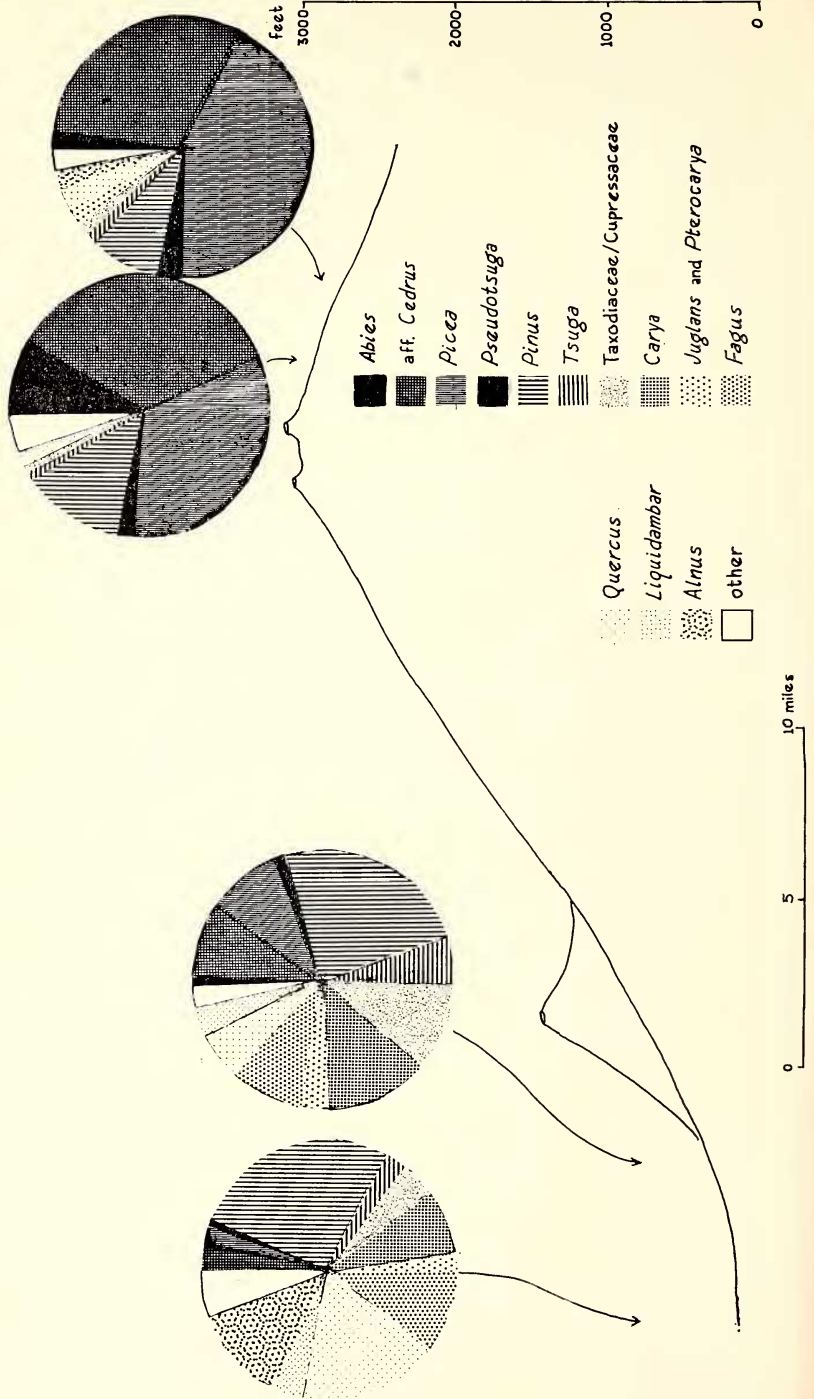


FIG. 2. Pollen spectra of some late Miocene assemblages in northwestern North America. The following assemblages are included (number preceding corresponds to figure 1; numbers in parentheses indicate number of samples and total grains counted): 25. Blue Mountains (2:600); 33. Hidden Lake (7:2112); 37. Mashel (1:300); 39. Pit River (1:300); 40. Pribilof Canyon (2:600); 41. Quesnel (1:430); 42. Skonun (10:1575); 44. Stewart Spring (1:300); 47. Thorn Creek (1:300); 48. Trapper Creek (1:300); 50. Type Homerian (6:1027); 51. Weyerhauser (3:964); Data for Quesnel furnished by K. M. Piel and data for Skonun from Martin and Rouse (1966). Some conifers are too sparsely represented in some spectra to be included in this illustration. Most of the solid black segment in Mashel spectrum represents *Keteleeria*. In the Pribilof Canyon spectrum Cy = Cyperaceae and Gramineae and in the Type Homerian spectrum Er = Ericales.



Pinus, Pinaceae are a minor element in the lowland spectra. Broad-leaved deciduous trees, notably members of Juglandaceae, Fagaceae, and *Liquidambar*, are dominant in the Weyerhauser spectrum and rare in the upland spectra. The Faraday spectrum is in some respects transitional between the Weyerhauser and the upland spectra. This transitional character could be expected because of the proximity to the site of deposition of the Faraday beds of a volcano that was active during the late Miocene (Peck, et al., 1964). The pollen profile for the Faraday beds displays a marked decrease in pollen of Pinaceae immediately above an ash layer; presumably the eruption of the ash from the local volcano resulted in the death of many Pinaceae that grew on the slopes of the volcano. Note that *Tsuga*, primarily *T. heterophylla* type, attains its highest relative abundance in the Faraday spectrum; *Tsuga* may have been a prominent member of the forest at altitudes intermediate between the Faraday and Hidden Lake sites of deposition.

The upland conifer forest, which can be characterized as a spruce-cedar forest, occupied a broad area from central British Columbia south to northeastern California and east to the mountains of Idaho. The Trapper Creek assemblages appears to be intermediate between the spruce-cedar association and the Nevada vegetation, as indicated in the Trapper Creek by the paucity of aff. *Cedrus* and the presence of *Ephedra*, *Sarcobatus*, and *Artemisia*. Axelrod (1964, p. 65) has suggested that the presence of *Ephedra* and *Sarcobatus* reported earlier from Trapper Creek (Leopold, in Mapel and Hail, 1959) was due to modern contamination. An additional sample, with which great care was taken to eliminate and prevent contamination, has also yielded these pollen types. There is no reasonable basis for the exclusion of these genera from the Trapper Creek flora.

The megafossil assemblages from Nevada have been characterized as representing a spruce-live oak-cedar (*Chamaecyparis*, not aff. *Cedrus*) association (Wolfe, 1964). The pollen assemblages from Stewart Spring that are now under study by H. E. Schorn confirms such an interpretation.

Judging both mega- and microfossil data, the following associations appear to have occupied northwestern North America during the late Miocene:

Alaska. Conifer forest of *Abies grandis*, *Picea sitchensis*, *P. glauca*, *Pinus monticola*, and *Tsuga heterophylla*, accompanied by *Betula papyrifera*, i.e., a birch-pine forest. Streamside vegetation largely Salicaceae and *Alnus*. Undergrowth largely Rosaceae and Ericaceae.

FIG. 3. Pollen spectra of some late Miocene assemblages in the Willamette Valley and Cascade Range of Oregon. Profile of Western Cascade Range is hypothetical but based on available geologic data (Peck, et al., 1965; D. L. Peck, pers. comm.). Assemblages are, from left to right (numbers in parentheses indicate number of samples and total grains counted): Weyerhauser (3:964), Faraday 28:7757), Skunk Creek (1:300) and Hidden Lake (7:2112). Small amounts of *Keteleeria* are included in the *Abies* totals.

Columbia Plateau-Cascade Range. Conifer forest of *Abies concolor*, *Abies magnifica*, aff. *Cedrus*, *Keteleeria*, *Picea breweriana*, *P. magna*, *Pinus monticola*, *P. ponderosa*, *Tsuga heterophylla*, *Thuja plicata*, and *Sequoia sempervirens*, accompanied by *Betula papyrifera*, *Quercus chrysolepis*, *Ulmus* spp., *Acer* spp., and *Arbutus idahoensis*, i.e., a spruce-cedar forest. Streamside vegetation largely Salicaceae, *Alnus*, and *Platanus*. Undergrowth mostly Rosaceae.

Nevada. Conifer forest of *Abies concolor*, *Picea breweriana*, *Picea magna*, *Chamaecyparis*, *nootkatensis*, *Tsuga heterophylla*, accompanied by *Quercus chrysolepis*, i.e., a spruce-cedar-live oak forest. Streamside vegetation largely Salicaceae. Undergrowth mostly Rosaceae.

Puget-Willamette lowland. Broad-leaved deciduous forest of *Carya bendirei*, *Fagus*, *Quercus deflexiloba*, *Liquidambar*, and *Arbutus*, accompanied by *Thuja plicata* and *Sequoia sempervirens*, i.e., a hickory-oak-beech forest. Streamside vegetation largely Salicaceae and Betulaceae. Undergrowth mostly Rosaceae and Ericaceae. Locally, a *Taxodium-Nyssa* association persisted.

Central California—mixed broad-leaved evergreen and deciduous woodland of *Quercus chrysolepis*, *Castanopsis*, *Carya*, *Persea*, and *Arbutus*, accompanied by *Pinus* (closed-cone), i.e., a live oak-madrone woodland. Streamside vegetation mostly Salicaceae. Undergrowth mostly Rosaceae and Ericaceae. Locally, a *Taxodium-Nyssa* association persisted.

PLIOCENE AND EARLY PLEISTOCENE

From about 10 to 2 or 3 million years ago, the fossil record in northwestern North America is notably poor. Pliocene assemblages are known in Alaska: the Type Clamgulchian, represented by many large collections from the Kenai Formation, and several assemblages from the Bering platform area (Hopkins, et al., 1960; Wolfe, unpublished data) that are probably of late Pliocene and/or early Pleistocene age. In the Pacific Northwest, Pliocene assemblages are represented by the Troutdale (Chaney, 1944b), Dalles (Chaney, 1944a), Middle Ellensburg (Smiley, 1963), and Deschutes (Chaney, 1938). One early Pleistocene assemblage is known from the Cape Blanco area (Wolfe unpublished data). Pliocene assemblages from regions south of the Pacific Northwest appear to have little to contribute to an understanding of the vegetation or flora of the Northwest.

The topographic setting of all the known Alaskan Pliocene and early Pleistocene assemblages is coastal lowland. The Troutdale assemblage in Oregon is the only Pliocene assemblage known from the Puget-Willamette lowland. The assemblages from eastern Washington and Oregon probably were at moderate elevations. The assemblage from the Elk River beds at Cape Blanco was obtained from rocks that are predominately marine.

FLORA. Compared to the Miocene, the Pliocene flora was depauperate. In Alaska, nearly all the broad-leaved deciduous trees had become ex-

tinct; note, however, that *Glyptostrobus*, which today is the most tropical member of Taxodiaceae, persisted into the Type Clamgulchian assemblage. Salicaceae and two species in the Betulaceae were the primary constituents of the Alaskan ligneous dicotyledonous flora, and Pinaceae are well represented by *Picea* and *Pinus* in the microfossil assemblages.

In the Northwest, the flora still contained some broad-leaved deciduous elements now exotic to the region, such as *Pterocarya*, *Ulmus*, *Platanus*, and *Aesculus*. Some of these exotics, e.g., *Ulmus*, are known in the Deschutes assemblage (Wolfe, unpublished data), which is only five to six million years old (Evernden and James, 1964). By the early Pleistocene, however, broad-leaved exotics were apparently almost extinct in the Northwest. The Elk River assemblage contains some *Platanus*, but otherwise the flora has a modern aspect.

The known megafossil species in the Northwestern Pliocene and Pleistocene assemblages are primarily members of lineages that were present in this region during the Miocene. No significant amount of migration of woody lineages into the region appears to have taken place during the Pliocene, although the fossil record is sufficiently poor to emphasize "appears." As noted in the discussion of the late Miocene flora, the flora of the Pacific Northwest was modern in aspect by the late Miocene.

VEGETATION. The character of the vegetation in the Northwest during the Pliocene is not clear, largely because of the lack of pollen assemblages and the small size of the megafossil assemblages. The leaf margin percentages for both the Troutdale and Middle Ellensburg show a definite increase compared to the Faraday and Lower Ellensburg. This change was not, therefore, the result of orogenic activity, because the Faraday-Troutdale sequence is west of the Cascade Range. The increase in leaf margin percentages is probably due to the onset of a definite summer dry climate in the Pacific Northwest (Wolfe and Hopkins, 1967). This change would account for the extinction of many lineages, e.g., those of *Carya*, *Fagus*, *Liquidambar*, and some of *Acer*. The persistence of *Ulmus* east of the Cascade Range should not be surprising, because some Asian species of the genus have proved to be highly successful in cultivation on the Columbia Plateau.

The Troutdale assemblage does not indicate a cooler climate than that of the late Miocene, despite the probable change to summer dry conditions. The extinction of various lineages by the end of the late Miocene can be readily explained in terms of the changed precipitation regime. Insofar as known, the Troutdale assemblage could represent broad-leaved deciduous forest derived from the late Miocene vegetation. None of the Troutdale localities have yielded records of Pinaceae more diverse than the Pinaceae of, for example, the Weyerhauser assemblage.

The Ellensburg assemblages (Smiley, 1963) may offer a clue as to the direction of temperature changes. The late Miocene Lower Ellensburg

assemblage lacks Lauraceae except for *Sassafras*, whereas the early Pliocene Upper Ellensburg assemblage contains *Persea*. Similarly, the Middle Ellensburg assemblage contains ligneous legumes lacking in the Lower Ellensburg. Although the evidence is not conclusive, the early Pliocene may have been somewhat warmer than the late Miocene in the Pacific Northwest.

The Deschutes assemblage indicates that by the later Pliocene, conifer forest was probably not present near the sites of deposition; the late Miocene rocks, however, consistently contain some megafossils of Pinaceae. This absence of Pinaceae in the Pliocene megafossil assemblages may reflect the increasing aridity from the rain shadow created by the accretion of the High Cascades. The conifer forest would thus be restricted to higher elevations away from the sites of deposition. Clearly, however, much more paleobotanical, especially palynologic, data are needed for an understanding of the vegetation of the Columbia Plateau during the Pliocene.

ORIGINS OF THE MODERN FLORA AND VEGETATION

From the preceding discussion, it is clear that many phylads and lineages now extant in the Pacific Northwest were present in this region prior to the Pleistocene and were in fact present in the Miocene. Several of the lineages were at one time members of the summer wet Mixed Mesophytic forest and have since adapted to summer dry conditions. Extant species that have such a history in the Pacific Northwest include: *Populus tremuloides*, *P. trichocarpa*, *Salix commutata*, *S. fluviatilis*, *S. lasianдра*, *S. lasiolepis*, *Quercus garryana*, *Q. kelloggi*, *Alnus rhombifolia*, *A. rubra*, *Betula occidentalis*, *Castanopsis chrysophylla*, *Celtis douglassi*, *Clematis columbiana*, *Mahonia aquifolium*, *M. repens*, *M. nervosa*, *Aemlanchier alnifolia*, *Cercocarpus montanus*, *Crataegus douglassi*, *Holodiscus discolor*, *Osmaronia cerasiformis*, *Peraphyllum ramoissimum*, *Prunus demissa*, *Sorbus scopulina*, *Spiraea, densiflora*, *Toxicodendron radicans*, *Acer grandidentatum*, *A. glabrum*, *A. macrophyllum*, *A. negundo*, *Ceanothus velutinus*, *Arbutus menziesi*, *Leucothoe davisae*, *Rhododendron occidentale*, *Cornus nuttalli*, *Garrya elliptica*, *Shepherdia utilis*, and *Sambucus glauca*.

Some of the extant species, however, appear to have entered the Pacific Northwest after the extinction of the Mixed Mesophytic forest, i.e., after the middle Miocene. Some appear to have entered from the north, because their first fossil records are in the Miocene or Pliocene of Alaska; note that this does not mean that the lineages are of northern origin but may have evolved in Eurasia and migrated through Alaska. Included are: *Salix barclayi*, *S. scouleriana*, *S. hookeriana*, *S. glauca*, *S. monticola*, *S. piperi*, *Myrica californica*, *Alnus, incana*, *A. sinuata*, *Ribes triste*, *Prunus subcordata*, *Rubus idaeus*, *Acer circinnatum*, *Gaultheria shallon*, *Vaccinium alaskaense*, and *Symphoricarpos albus*.

The majority of these species live today in the mountains of the

Pacific Northwest, although some, particularly *Salix hookeriana* and its allies, are lowland species. These willows apparently attained a coastal distribution from Cook Inlet south to western Washington during the later Miocene. Some lineages may have entered the Pacific Northwest from the south. *Peraphyllum*, for example, was a member of the Mixed Mesophytic forest in the Northwest, but the only late Miocene record of the genus is in Nevada; when summer dry climates prevailed in the Northwest at the close of the Miocene, lineages such as *Peraphyllum* may have reentered from the south. Most "Madro-Tertiary" elements in the modern flora of the Northwest may have followed such a pattern.

The known Tertiary vegetation of the Pacific Northwest does not closely match the modern vegetation floristically. The deciduous broad-leaved forest of the late Miocene western lowlands has survived in a highly modified form in the Willamette and Rogue River valleys. At least 50 percent of the late Miocene species of this vegetation, however, no longer participate in this forest type. Most have become regionally extinct, but others, for example, *Leucothoe* aff. *L. davisae*, are today montane species.

The late Miocene conifer forest of the Columbia Plateau-Cascade region has also been highly modified since 10 million years ago. The area perhaps floristically most closely related to this vegetation is the present Siskiyou Mountains and adjacent areas. In this region, most of the late Miocene conifer species have survived, including some of the associated ligneous dicotyledons. Again, however, at least 50 percent of the late Miocene species associated with the conifer forest no longer participate in this extant forest type. Although extinction accounts for much of the floristic change, some of the lineages, e.g., those to which *Quercus chrysolepis* sensu stricto (excluding *Q. vaccinifolia*) and *Plantanus racemosa* belong, are no longer part of the conifer forest. The primary difference, however, between the late Miocene and modern conifer forest of the Northwest is that *Pseudotsuga* did not play as significant a role in the vegetation as it does today. Hansen's (1949) data indicate that *Pseudotsuga* pollen in the pollen rain occurs in about the same percentage as the percentage of *Pseudotsuga* in the surrounding forest as measured in basal area. Pollen of *Pseudotsuga* is, however, not abundant in any Neogene pollen assemblage known to me in the Northwest. Even the early Pleistocene assemblages at Cape Blanco have low amounts of *Pseudotsuga* (Wolfe, unpublished data), whereas interglacial deposits of the Puget lowland (Leopold, unpublished data) contain large quantities of the genus. It appears, therefore, that the dominance of *Pseudotsuga* in the present conifer forest of the Northwest was attained during the middle or late Pleistocene.

Note also that, since the late Miocene, the conifer forest has received some immigrants from the north as well as incorporating some elements from the late Miocene broad-leaved forest. To the latter group probably

belong: *Arbutus menziesi*, *Leucothoe davisae*, and *Rhododendron macrophyllum*.

The conifer forest of the late Miocene of Alaska has, of course, suffered from extensive extinction. Vegetationally, this conifer forest is probably most like that of southern British Columbia, and there are also strong floristic similarities. The apparent absence of *Acer* and *Rhododendron* (*Rhododendron*) coupled with the presence of *Pterocarya* and *Ulmus* in the Alaskan late Miocene, however, indicate that as a vegetational and floristic unit the Alaskan late Miocene forest did not migrate southward.

The floristic changes that have occurred in the vegetation of the Pacific Northwest during the Neogene indicate strongly that the present associations are also most probably transitory. As Mason (1947) has noted, the association must be continually redefined at each point in time because of the coincidental nature of associations.

U.S. Geological Survey, Menlo Park, California

LITERATURE CITED

- AXELROD, D. I. 1956. Mio-Pliocene floras from west-central Nevada. Univ. Calif. Publ. Geol. Sci. 33.
- . 1962. A Pliocene Sequoiadendron forest from western Nevada. Univ. Calif. Publ. Geol. Sci. 39:195-268.
- . 1964. The Miocene Trapper Creek flora of southern Idaho. Univ. Calif. Publ. Geol. Sci. 51.
- BAILEY, I. W., and E. W. SINNOTT. 1915. A botanical index of Cretaceous and Tertiary climates. Science 41:831-834.
- . 1916. The climatic distribution of certain types of Angiosperm leaves. Amer. J. Bot. 3:24-39.
- BERRY, E. W. 1931. A Miocene flora from Grand Coulee, Washington. U.S. Geol. Surv. Prof. Paper 170-C.
- BROWN, R. W. 1940. New species and changes of name in some American fossil floras. J. Wash. Acad. Sci. 30:344-356.
- BURK, C. A. 1965. Geology of the Alaska Peninsula—Island arc and continental margin (Part I). Geol. Soc. Amer. Mem. 99.
- CAIN, S. A. 1944. Foundations of plant geography. Harper, New York.
- CHANEY, R. W. 1920. The flora of the Eagle Creek Formation. Contr. Walker Mus. 2:115-181.
- . 1924. Quantitative studies of the Bridge Creek flora. Amer. J. Sci. 8:127-144.
- . 127. Geology and paleontology of the Crooked River basin with special reference to the Bridge Creek flora. Publ. Carnegie Inst. Wash. 346:45-138.
- . 1938. The Deschutes flora of eastern Oregon. Publ. Carnegie Inst. Wash. 476:187-216.
- . 1944a. The Dalles flora. Publ. Carnegie Inst. Wash. 553:285-321.
- . 1944b. The Troutdale flora. Publ. Carnegie Inst. Wash. 553:323-351.
- . 1952. Conifer dominants in the middle Tertiary of the John Day basin, Oregon. Paleobotanist 1:105-113.
- . 1959. Miocene floras of the Columbia Plateau. Part I. Composition and interpretation. Publ. Carnegie Inst. Wash. 617:1-134.
- , and D. I. AXELROD. 1959. Miocene floras of the Columbia Plateau. Part II. Systematic considerations. Publ. Carnegie Inst. Wash. 617:135-237.

- CHELEBAEVA, A. I. 1968. The Neogene flora of the River Pirozhnikovaya in Kamchatka. [In Russian.] *Bot. Zurn.* (Moscow & Leningrad) 53:737-748.
- CONDIT, C. 1938. The San Pablo flora of west-central California. *Publ. Carnegie Inst. Wash.* 476:217-268.
- . 1944. The Table Mountain flora. *Publ. Carnegie Inst. Wash.* 553:57-90.
- DAVIS, M. B., and J. C. GOODLETT. 1960. Comparison of the present vegetation with pollen-spectra in surface samples from Brownington Pond, Vermont. *Ecology* 41:346-357.
- DORF, E. 1936. A late Tertiary flora from southwestern Idaho. *Publ. Carnegie Inst. Wash.* 476:73-124.
- EVERNDEN, J. F., and G. T. JAMES. 1964. Potassium-argon dates and the Tertiary floras of North America. *Amer. J. Sci.* 262:945-974.
- , D. E. SAVAGE, G. H. CURTIS, and G. T. JAMES. 1964. Potassium-argon dates and the Cenozoic mammalian chronology of North America. *9mer. J. Sci.* 262:145-198.
- FÆGRI, K., and J. IVERSEN. 1964. *Textbook of pollen analysis.* Hafner, New York.
- GRAHAM, A. 1965. The Sucker Creek and Trout Creek Miocene floras of southeastern Oregon. *Kent State Univ. Bull.* 53.
- GRAY, J., and L. R. KITTLEMAN. 1967. Geochronometry of the Columbia River basal and associated flora of eastern Washington and western Idaho. *Amer. J. Sci.* 265:257-291.
- HANSEN, H. P. 1949. Pollen content of moss polsters in relation to forest composition. *Amer. Midl. Naturalist* 42:473-479.
- HOPKINS, D. M., F. S. MACNEIL, and E. B. LEOPOLD. 1960. The coastal plain at Nome, Alaska: a late Cenozoic type section for the Bering Strait region. *Rep. 21st Int. Geol. Congr.* pt. 4:46-57.
- , D. W. SCHOLL, W. O. ADDICOTT, R. L. PIERCE, P. J. SMITH, J. A. WOLFE, D. GERSHANOVICH, B. KOTONEV, K. E. LOHMAN, and J. OBRADOVICH. In press. Cretaceous, Tertiary, and early Pleistocene rocks from the continental margin in the Bering Sea. *Bull. Geol. Soc. Amer.*
- KNOWLTON, F. H. 1902. Fossil flora of the John Day basin, Oregon. *U.S. Geol. Surv. Bull.* 204.
- LAMOTTE, R. S. 1936. The Upper Cedarville flora of northwestern Nevada and adjacent California. *Publ. Carnegie Inst. Wash.* 455:57-142.
- MACGINITIE, H. D. 1953. Fossil plants of the Florissant beds, Colorado. *Publ. Carnegie Inst. Wash.* 599.
- MASON, H. L. 1947. Evolution of certain floristic associations in western North America. *Ecol. Monogr.* 17:201-210.
- MAPEL, W. J., and W. J. HAIL. 1959. Tertiary geology of the Goose Creek district, Cassia County, Idaho, Box Elder County, Utah, and Elko County, Nevada. *U.S. Geol. Surv. Bull.* 1055-H.
- MARTIN, H. A., and G. E. ROUSE. 1966. Palynology of late Tertiary sediments from the Queen Charlotte Islands, British Columbia. *Canad. J. Bot.* 44:171-208.
- PARDEE, J. T., and K. BRYAN. 1926. Geology of the Latah formation in relation to the lavas of the Columbia Plateau near Spokane, Washington. *U.S. Geol. Surv. Prof. Paper* 140-A:1-16.
- PECK, D. L., A. B. GRIGGS, H. G. SCHLICKER, F. G. WELLS, and H. M. DOLE. 1964. Geology of the central and northern parts of the Western Cascade Range in Oregon. *U.S. Geol. Surv. Prof. Paper* 449.
- RICHARDS, P. W. 1952. *The Tropical Rain Forest.* Cambridge Univ. Press.
- SMILEY, C. J. 1963. The Ellenburg flora of Washington. *Univ. Calif. Publ. Geol. Sci.* 35:159-276.
- SMITH, H. V. 1941. A Miocene flora from Thorn Creek, Idaho. *Amer. Midl. Naturalist* 25:473-522.
- SOKAL, R. R., and P. H. A. SNEATH. 1963. *Principles of Numerical Taxonomy.* Freeman, San Francisco.

- THAYER, T. P., and C. E. BROWN. 1966. Geologic map of the Aldrich Mountain quadrangle, Grant County, Oregon. U.S. Geol. Surv. Map GQ-438.
- TURNER, D. L. 1968. Potassium argon dates concerning the Tertiary foraminiferal time scale and San Andreas fault displacement. Ph.D. thesis. Univ. Calif., Berkeley.
- WAHRHAFTIG, C., J. A. WOLFE, E. B. LEOPOLD, and M. A. LANPHERE. 1969. The coal-bearing group in the Nenana coal field, Alaska. U.S. Geol. Surv. Bull. 1274-D.
- WANG, CHI-WU. 1961. The forests of China. Pub. Maria Moors Cabot Found. Bot. Res. 5.
- WOLFE, J. A. Tertiary Juglandaceae of western North America. M.A. thesis. Univ. Calif., Berkeley.
- . 1960. Early Miocene floras of northwest Oregon. Ph.D. thesis. Univ. Calif., Berkeley.
- . 1962. A Miocene pollen sequence from the Cascade Range of northern Oregon. U.S. Geol. Surv. Prof. Paper 450-C:C81-C84.
- . 1964. Miocene floras from Fingerrock Wash, southwestern Nevada. U.S. Geol. Surv. Prof. Paper 454-N.
- . 1966. Tertiary plants from the Cook Inlet region, Alaska. U.S. Geol. Surv. Prof. Paper 398-B.
- . 1968. Paleogene biostratigraphy of nonmarine rocks in King County, Washington. U.S. Geol. Surv. Prof. Paper 571.
- . 1969. Paleogene floras from the Gulf of Alaska region. U.S. Geol. Surv. open-file report.
- , and D. M. HOPKINS. 1967. Climatic changes recorded by Tertiary land floras in northwestern North America. *In* K. Hatai, Tertiary correlation and climatic changes in the Pacific. Sasaki, Sendai, Japan.
- , D. M. HOPKINS, and E. B. LEOPOLD. 1966. Tertiary stratigraphy and biostratigraphy of the Cook Inlet region, Alaska. U.S. Geol. Surv. Prof. Paper 398-A.
- , and E. B. LEOPOLD. 1967. Neogene and early Quaternary vegetation of northwestern North America and northeastern Asia. *In* D. M. Hopkins, ed., The Bering Land Bridge. Stanford Univ. Press, Stanford.